

megasporangiate fructifications, or isolated megasporangiate organs could be assigned to families. All other organs are then described as satellite taxa assigned either to a family or to an order, as seems most appropriate in each case. (2.) An assumption that placing different species in the same genus implies phylogenetic relationship rather than mere phenetic similarity can influence the conception of plant communities, distribution patterns, and paleogeography. (3.) It is difficult to know whether many specimens are from herbaceous or arborescent lycopoids, and it is easy to make assumptions that are untestable on limited evidence.

When further evidence is found of larger, more complete, specimens, or of attached reproductive organs, the possible interpretations must be treated with care. For example, the Lower Carboniferous European genus *Eskdalia* Kidston emend Thomas & Meyen (1984b), also described from South Africa (Brown & Lemoigne, 1977) and Siberia (Thomas & Meyen, 1984b), has generally been regarded as a taxon of comparatively small lycopoids (Thomas, 1968; Meyen, 1976; Thomas & Meyen, 1984b). Rowe (1988a), however, redescribed and renamed some specimens of *Scutellocladus variabilis* Lele & Walton (1962) from the Visean Drybrook Sandstone of the Forest of Dean, Gloucestershire, United Kingdom, as *E. variabilis*, which he believed to be the terminal shoots of an arborescent lycopoid because of its branching pattern and its possession of terminal cones. This species underlines the dangers of making generalized inferences from comparison of species based on vegetative axes. The type specimens of *Eskdalia variabilis* were originally assigned to the monotypic genus *Scutellocladus* Lele & Walton (1962), but were later included in *Tomiodendron* Radczenko emend. Meyen, 1972, by Thomas & Purdy (1983); a genus that has also been described from Alaska (Spicer & Thomas, 1987), North Africa (Lejal-Nicol & Massa, 1980) and Siberia (Meyen, 1976). The use of either of the widely distributed genera *Eskdalia* or *Tomiodendron* for these fertile British Visean shoots could be misinterpreted as implying that all species included within it are taxa of the terminal branches of arborescent lycopoids. *Scutellocladus*, redefined to include the terminal reproductive organs, should not be misinterpreted in this way.

THE BEGINNINGS OF MODERN HERBACEOUS LYCOPSIDS

What then can be interpreted from the fossil record that might give some indication of the evolutionary relationships within the herbaceous ly-

copsids, or the evolutionary history of the modern herbaceous genera *Selaginella* sens. lat. and *Lycopodium* sens. lat.?

Available evidence suggests that the extant herbaceous lycopoids most probably had their origins in the same Upper Carboniferous equatorial region where the arborescent lycopoids were reaching their zenith. In contrast with the Euramerican equatorial region, the northern Angaran Upper Carboniferous and Permian floras showed increasing endemism. There were large numbers of lycopoids in the Angaran Carboniferous that Meyen (1972) described as a cheerless and monotonous "brush" of fairly short straight sticks and suggested that the scanty vegetation was associated with lakes and rivers. There were no truly herbaceous forms; the lycopoids were represented by such genera of shrubby plants as *Lophiodendron* Zalessky, 1936, *Tomiodendron* Radczenko emend. Meyen, 1972, *Angarophloios* Meyen, 1972, *Ursodendron* Radczenko emend. Meyen, 1972, *Angarodendron* Zalessky, 1918, *Tunguskadendron* Thomas & Meyen, 1984c, and *Eskdalia* Kidston emend Thomas & Meyen, 1984b.

Similarly, there were no herbaceous forms in the Upper Paleozoic tundra vegetation of Gondwanaland (Retallack, 1980). There were instead very small trees or shrubs such as the Argentinian *Bumbudendron* and *Malanzania* described by Archangelsky et al. (1981) and the Brazilian Permian *Brasilodendron* Chaloner et al., 1968. Archangelsky et al. (1981) showed that *Bumbudendron paganzianum* had fertile branch structures rather than strobili, and Chaloner et al. (1968) suggested similar fertile structures for *Brasilodendron pedroanum*. Such simple reproductive structures were common world-wide in the Lower Carboniferous but later seem to have become restricted to the equatorial belt.

HOMOSPORY

Lycopodites Brongniart, 1822, or *Lycopodites* Lindley & Hutton, 1833, is a name that has been given to small, presumed herbaceous, leafy lycopoid shoots. Species based on vegetative axes alone have also been included. Pal & Ghosh (1990) have discussed the problems emanating from Brongniart's (1822) use of *Lycopodites* for a type species whose affinities are confused and argued the case for preferring Lindley & Hutton's usage of the generic name.

Species of *Lycopodites* have been described from the Upper Devonian onward and some of these are known to be fertile. For example, *Lycopodites*

oosensis Kräusel & Weyland, 1937, from the Upper Devonian of Germany has globose sporangia on unspecialized sporophylls and spores that are 90–120 μm in diameter. Other species are merely vegetative shoots with no indication of their reproductive organs. Some of these vegetative shoots assigned to *Lycopodites* are isophyllous, such as *L. pendulus* Lesquereux, 1880, from the Upper Carboniferous of Illinois, U.S.A., *L. arberi* Edwards, 1934, from the Jurassic of New Zealand and *Lycopodites hannahensis* Harris, 1976, from the English Wealden. This last species, based on a large number of erect, dichotomizing vegetative stems preserved in a fine-grained sandstone was interpreted by Harris as a slender, upright, reedlike plant. I have found a similar specimen in fine-grained sandstone in the Yorkshire Jurassic. Such plants might well have been common on sandy mud flats on riverbanks and deltas throughout the Mesozoic. Other species of *Lycopodites* are anisophyllous, possessing two lower ranks of larger leaves and two upper ranks of smaller leaves. The type species, *L. falcatus* Lindley & Hutton (1833; re-examined by Harris, 1961), is of this form. This character is not restricted in extant species to *Selaginella*; there is a form of anisophylly occasionally present in *Lycopodium* resembling that of *Selaginella* (e.g., *Lycopodium carolinianum* figured in Troll, 1937). This clearly has implications for the use of anisophylly as an aid to generic distinction, and the problem will be discussed later in the section on the "generic assignment of herbaceous fossil lycopsids."

Carinostrobus foresmanii was the name given by Baxter (1971) to a single lycopsid cone from the Pennsylvanian of Kansas. It was only 2.3–3.0 mm in diameter, suggesting that it might have been the fructification of an herbaceous species. The spores were all of one type and 20–22 μm in diameter, indicating that the cone was either homosporous, microsporangiate, or a fragment of a heterosporous cone. Baxter, however, stated that *Carinostrobus* clearly lacked a ligule. Unfortunately, we have no knowledge of the plant that bore the cone.

HETEROSPORY

Heterospory is presumed to have developed in several groups of plants during the late Devonian, for the record of fossil spores shows a rapid increase in the number and diversity of presumed megaspores during this period (e.g., Chaloner, 1967). A few heterosporous Devonian fructifications probably belong to herbaceous lycopsids. For example, *Barsostrobus famennensis* Fairon-Demaret (1977)

from the Upper Devonian of Belgium is an isolated portion of a cone with narrowly triangular and toothed sporophylls, each bearing a stalked, slightly reniform sporangium. The spores are all 240–320 μm in diameter and are interpreted as small megaspores. However, no ligules have been observed. These morphological characters, and details of its anatomy and vascular bundles, suggest that *B. famennensis* is closer to Carboniferous lycopsids than to the early Devonian forms. Unfortunately, once again the vegetative organs of the plant are unknown.

Other herbaceous forms from the Euramerican Upper Carboniferous Coal Measures were very similar to extant species of *Selaginella*. Some are known to have been heterosporous, but others are known to resemble *Selaginella* only in morphological characters of vegetative shoots. Both isophyllous and anisophyllous species are known from the Carboniferous onward.

The fairly rare anisophyllous shoots either have been placed into *Lycopodites* (as mentioned above), included in the genus *Selaginellites* Zeiller, 1906, or even regarded as species of *Selaginella* sens. str. *Selaginellites* was first used by Zeiller for a specimen from the Upper Carboniferous of the Blanzky Coalfield, France that he named *Selaginellites suissei*. This lycopsid had a dichotomously branched stem, dimorphic leaves, and a distinctive bisporangiate cone with apical microsporangia and basal megasporangia. *Selaginellites suissei* is therefore very similar to many living anisophyllous species of *Selaginella* that have tetragonous strobili (e.g., *Selaginella vogellii* Spring, *S. cathedrifolia* Spring and *S. pervillei* Spring: Quansah, 1988).

There are several other species of anisophyllous *Selaginellites* that have been described from the Carboniferous Coal Measures. I have reexamined the remarkable specimen of *Selaginellites gutbieri* (Goeppert) Kidston, 1911, from the Westphalian D of the Zwickau Coalfield, Poland, which was refigured by both Schimper (1870–1872, pl. 57, fig. 4) and Hirmer (1927, fig. 327). It is truly anisophyllous with terminal cones. Microspores (of the *Ciratriradites* form) were recovered from several of the cones, although megaspores were not found. It is, however, quite possible that the plant had only microsporangia similar to the condition found in some individuals of many living anisophyllous species of *Selaginella* (e.g., *S. versicolor* Spring, *S. vogellii* Spring and *S. leonensis* Hieron. (Quansah, 1988)). *Selaginellites elongata* Goldenberg, 1855, is, however, rather different. It was reexamined by Halle (1907), who described

the sporangia as occurring in the axils of ordinary vegetative leaves. This condition is found in living species such as *Selaginella denticulata* (L.) Link and *S. pallidissima* Spring, where there are two sizes of sporophylls arranged in four ranks. In these living species the smaller sporophylls are in the same plane as the smaller median vegetative leaves, and the larger sporophylls are in the same plane as the larger lateral vegetative leaves (Quansah, 1986). This gives the superficial appearance of there not being a discrete cone. Kidston (1911) also described some fertile specimens from the Westphalian B of the Belgium Coalfield as *Selaginellites gutbieri*, although his plate figures are labeled as *S. primaevus* Goldenberg. There are, however, several characters that distinguish the Belgian cones from *S. gutbieri*. The most obvious differences are that the larger leaves are much more dentate and the sporophylls are approximately the same size as the larger vegetative leaves. It is therefore very similar to *S. elongata*, although a reexamination of the Belgian material is necessary before any firm identification can be made.

I have also seen other specimens of late Carboniferous herbaceous anisophyllous shoots, from Poland and Germany, that have distinctly different leaf shapes, leaf orientations and leaf outlines. Such characters are remarkably consistent in living species of *Selaginella* (Quansah, 1986; Dahlen, 1988), so it is reasonable to assume that they can be used for distinguishing species of fossils.

Anisophyllous forms have also been described from Mesozoic strata, and many of these have been shown to be heterosporous; examples include *Selaginella anasazia* Ash, 1972, from the Trias of New Mexico, *Selaginella hallei* Lundblad, 1950b, from the Rhaetic of Sweden and *Selaginella dawsoni* Watson, 1969, from the Wealden of England. There are also vegetative shoots such as *Selaginella dichotoma* Velenovsky & Viniklav, 1931, from the Jurassic of Siberia and *Selaginellites nosikovii* from the Cretaceous of Czechoslovakia.

The earliest isophyllous specimens of *Selaginella* (= *Selaginellites*) are known from the Lower Carboniferous. These, called *Selaginellites resimus* Rowe (1988b), came from the Drybrook Sandstone. They are both herbaceous and isophyllous, with small terminal strobili showing impressions of megaspores in several sporangia.

Isophyllous forms such as *Selaginella fraipontii* (Leclercq) Schlanker & Leisman, 1969, are also known from the Upper Carboniferous Euramerican Coal Measures, although they are similarly rare. This species has been described as sparsely branched, sprawling and possibly of determinate

growth. The terminal cones had sporophylls arranged in alternating pairs of verticels. It is very similar in morphology to some extant species of *Selaginella* (e.g., *S. selaginoides* L.), except for not having a distinctive basal root-bearing organ. It also shows a very close similarity in stelar anatomy, change in the number of protoxylem points, secondary growth in the base of the stem, and in the change from centrarch to exarc steles.

Isolated cones are also included in *Selaginellites*, such as *S. polaris* Lundblad, 1948, from the Trias of Greenland. We know nothing of their axes, and their assignment to this genus is therefore tenuous.

Miadesmia membranacea Bertrand (Benson, 1908) is an isolated cone of a rather different structure. Its small size suggests that it might belong to an herbaceous lycopoid, although there is no other evidence. It is megasporangiate: a single large megaspore occupies each sporangium, which in turn is enclosed by integuments, suggesting an analogy in its structure with that of *Lepidocarpon* Scott, 1900.

THE GENERIC ASSIGNMENT OF HERBACEOUS FOSSIL LYCOPSIDS

Lycopodites is generally used to encompass homosporous lycopoids, or just vegetative axes, bearing a resemblance to living species of *Lycopodium*. Although the usage of the name *Lycopodites* varies, there is no strong argument for any of the fossils to be included within *Lycopodium* sens. str. *Lycopodites* seems to be a problematic taxonomic unit; some specimens have even been subsequently shown to be twigs of larger lycopoids or even of conifers. When Harris (1961) redescribed the type species of *Lycopodites*, *L. falcatus* Lindley & Hutton (see Pal & Ghosh, 1990, for a discussion on generic priority), from the Yorkshire Jurassic, he not only confirmed its anisophyllous structure but showed there to be twice as many larger lateral leaves as smaller leaves. *Lycopodites falcatus* was, however, solely vegetative. It might therefore be better to consider restricting the use of *Lycopodites* to that of a form-genus of sterile axes and to accept that it is delimited by artificial parameters. Harris's (1969) classification of Mesozoic conifer shoots offers a precedent for this practice.

There has, however, been intense debate about the necessity of using another generic name in preference to *Selaginella* for fossil plants resembling this genus. Zeiller (1906) originally suggested that the presence of more than four megaspores in each megasporangium was a distinguishing char-

acter of his new genus *Selaginellites*. Halle (1907) did not accept that this character was essential and used *Selaginellites* for all heterosporous fossils. Subsequently, Duerden (1929) and Quansah (1988) showed that living species of *Selaginella* can possess more than four megaspores per sporangium. Seward (1910), Harris (1935), Hirmer (1941), Chaloner (1967), and Rowe (1988a) used *Selaginellites* for all fossil shoots that were closer to *Selaginella* than any other genus. In contrast, Darrah (1938), Lundblad (1950b), Townrow (1968), Schlanker & Leisman (1969), Watson (1969), and Ash (1972) used *Selaginella* for fossil shoots because they could not demonstrate any real morphological differences from the extant species of that genus. The problem of using generic names of extant plants for fossil specimens is a major one encountered throughout palaeobotany (e.g., Collinson, 1986). In the case of the herbaceous anisophyllous axes, further complications can arise during attempts to include fossil species of *Selaginella* in the described subgenera, or to incorporate them into the various genera suggested for splitting *Selaginella*. This problem will be discussed in the following section.

Fossil plants are usually incomplete fragments of whole organisms, which pose even more problems for generic assignment. For example, Lundblad (1948) assigned a small detached heterosporous cone to *Selaginellites* with no knowledge of vegetative morphology, even though the cone was broader than those of all living species of *Selaginella*. This approach may be the simplest way of dealing with the situation but, when the fossils are merely vegetative axes, taxonomic decisions have to be made without knowledge of their reproductive organs.

It is interesting to note how the use of these generic names can vary, even within a single publication. For example, Lundblad (1950a) named an isolated cone from the Rhaetic of Sweden *Selaginellites hallei* sp. nov. but referred the associated vegetative, anisophyllous axes to *Lycopodites scanicus* Nathorst ex Halle. Later, Lundblad (1950b) found fertile specimens sharing the characters of both these species and named them *Selaginella hallei* comb. nov., presumably preferring to use the cone name rather than taxonomically uniting the two species and using the rules of priority (cf. Greuter et al., 1988).

Many systematists have followed Bower (1935) in arguing that *Selaginella selaginoides* L. is a primitive form because of its radial construction and the lack of aerial roots. However, the anisophyllous heterosporous forms appeared in the fossil

record soon after the isophyllous forms, implying that plants with the *Selaginella selaginoides* morphological form may not be ancestral to all *Selaginella*-like fossils. It is possible that an ancestral group of both the isophyllous and anisophyllous lycopsids might be eventually recognized in the late Devonian or very early Carboniferous lycopsids. However, it is also possible that these plants are much less closely related than has been previously thought.

FOSSIL EVIDENCE FOR THE GENERIC ASSIGNMENT OF THE EXTANT SPECIES OF THE SELAGINELLACEAE

Early classifications (e.g., Willdenow, 1810; Sprengel, 1827) placed *Selaginella* within the genus *Lycopodium*, though Spring (1850) presented the major monograph of the genus *Selaginella* as it is presently understood. Even though most workers have generally understood and agreed on the parameters delimiting the genus *Selaginella*, there have been many attempts to express taxonomically groups of species that have distinctive morphologies. The taxonomic divisions of the genus by various authors differ in the number of subgenera or genera that they accept.

A study of African species of *Selaginella* (Quansah, 1986) and a preliminary review of approximately 100 South American species (Quansah & Thomas, 1985) suggest that the genus should be divided into at least two genera or subgenera: those with isophyllous leaves and those with anisophyllous leaves. This is supported by several recent studies, including Jermy et al. (1967), Crabbe & Jermy (1976), Alston et al. (1981), and Tryon & Tryon (1981), whose authors have recognized two subgenera, *Selaginella* and *Stachygynandrum*, within the genus. The two groups originate from Baker's (1883, 1887) classification. The other two subgenera, recognized by Baker and by Walton & Alston (1938), *Homostachys* and *Heterostachys*, are best recognized at a lower hierarchical level within the group containing all the anisophyllous species.

Jermy (1986) has, however, proposed five subgenera within *Selaginella*. The two subgenera of anisophyllous species differ in several characters, including their cone morphologies. It is interesting to note that Carboniferous *Selaginellites* could be included in both of these subgenera; *S. gutbieri*, with its uniform and tetrastichous sporophylls, could be included in Jermy's subgenus *Stachygynandrum* (P. Beauv.) Baker, while the Carboniferous *Selaginellites elongata* could be included in Jermy's subgenus *Heterostachys* Baker. Work in

progress on the Carboniferous species may give further evidence in support of Jermy's idea of creating five subgenera.

It is, at least, clear that both isophyllous and anisophyllous *Selaginella*-like plants are known from the Carboniferous onwards and that some of these have been thought even to be generically indistinguishable from extant *Selaginella*. The origin of isophyllous and anisophyllous lycopoids at approximately the same point in geological time can be taken as additional evidence for regarding the two groups of plants as taxonomically distinct. Indeed, the recognizable division into two different morphologies, which has existed for approximately 300 million years, strengthens considerably the argument for making the division at generic rather than subgeneric level.

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DEVELOPMENTAL PROBLEMS *Terry R. Webster*² IN *SELAGINELLA* (SELAGINELLACEAE) IN AN EVOLUTIONARY CONTEXT¹

ABSTRACT

The antiquity and diversity of *Selaginella* species attest to the evolutionary success of the genus. This success may be attributed, in part, to certain morphological and anatomical features that characterize *Selaginella*. Recent developmental studies of anisophylly, monoplastidy, the ligule, the rhizophore, marginal warty cells, and marginal teeth of the leaves, as well as aspects of the heterosporous life cycle are discussed. Unresolved questions concerning vegetative features include the function of the ligule, morphological interpretation of the so-called rhizophore, and a possible role of distinctive leaf ornamentations in water economy. Among unresolved questions concerning reproductive morphology are the basis of heterospory, control of sporangial development, spore dispersal mechanisms as they affect inbreeding and outcrossing, and other details of the reproductive process. It is concluded that the genus *Selaginella* offers numerous opportunities for future research.

From the standpoint of both development and evolution, the genus *Selaginella* raises a number of intriguing questions. In this regard the following quotation from Bierhorst (1971) seems appropriate:

The family Selaginellaceae includes *Selaginella* and several very closely related fossil forms which are known from Lower Carboniferous and more recent strata. *Selaginella* is probably one of the oldest of all extant genera of vascular plants, second only to *Lycopodium*. Despite its great antiquity, which might lead one to expect specialization and relative genetic stagnation, there are approximately 700 extant species and much evidence for recent speciation.

The key elements of this statement are the antiquity and diversity of the genus and the probability that *Selaginella* is presently undergoing active speciation. Years ago, the prominent morphologist C. W. Wardlaw (1925) also alluded to the evolutionary status of *Selaginella*:

The genus is represented by a large number of species, many of which are polymorphic. They have a wide geographical distribution, and in some floras they dominate the ground vegetation. Further, they show adaptation to all degrees of xerophily and hygrophily. It would appear from these facts that the genus is successfully retaining its position in the midst of the more highly differentiated Phanerogams.

With our current state of knowledge, the reasons for the apparent evolutionary success exhibited by

Selaginella are far from obvious. It is my contention that, at least in part, the reasons may be found in the genus's unique combination of vegetative and reproductive features. These include anisophylly, the ligule, the presence of certain foliar epidermal ornamentations, the aerial root (rhizophore), monoplastidy, and certain aspects of the heterosporous life cycle (Fig. 1). It should be emphasized that although each of these features may be found in other plant groups (for example, the ligule is found in *Isoetes* as well as in *Selaginella*), it is the combination of features that is unique to *Selaginella*. It is the purpose of this paper to discuss these features and to point out certain controversies and questions, which may lead to further discussion and future studies. Although some older references from the literature have been included where appropriate, this paper mainly considers work of the past 30 years.

VEGETATIVE MORPHOLOGY

Certain vegetative features of *Selaginella* have intrigued students of the genus for many years. For example, the ligule and the so-called rhizophore are two enigmatic structures that are familiar to students of plant morphology. Yet, despite numerous studies, the morphological interpretation and evolutionary significance of many of the vegetative features of *Selaginella* remain a mystery. An examination of the vegetative plant body reveals

¹ The author thanks M. J. Spring for preparing the illustrations in Figure 1.

² Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3043, U.S.A.

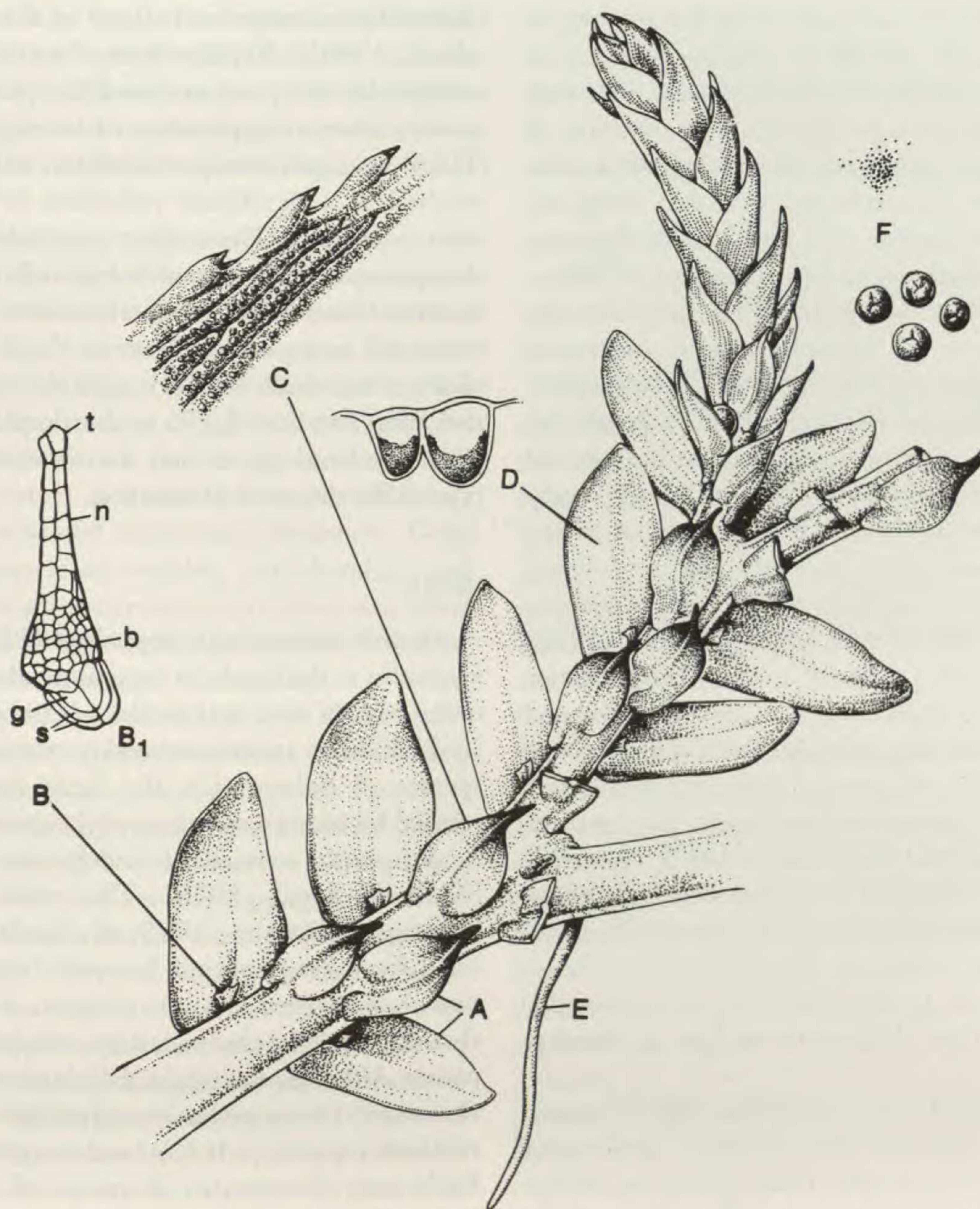


FIGURE 1. Diagram of structural features of *Selaginella*.—A. Anisophylly.—B. Ligule.—B1. Ligule, in section. t = tip, n = neck, b = base, g = glossopodium, s = sheath.—C. Marginal warty cells and marginal teeth.—D. Monoplastidy.—E. Aerial root (rhizophore).—F. Heterospory.

a basic simplicity of design, which would seem to make the evolutionary success exhibited by the genus that much more interesting. A critical examination of certain key vegetative features may provide insights into this apparent contradiction.

ANISOPHYLLY

Perhaps the most obvious vegetative feature found in most species of *Selaginella* is anisophylly. According to Dengler (1983a), the term anisophylly refers to differences in leaf form related to the transectional symmetry of the shoot and most often occurs in plagiotropic shoots from shaded situations in which the foliage leaves on the upper side of the stem are smaller than those on the lower side. In several detailed studies, Dengler (1980,

1983a, b) investigated anisophylly in *S. martensii*. Unlike many plants that are anisophyllous, *Selaginella* (sect. *Heterophyllum*) exhibits no transitional leaf forms, but rather shows two distinct leaf types borne in pairs along the stem. At each node one smaller dorsal leaf and one larger ventral or lateral leaf are initiated as an opposite pair (Fig. 1). Leaf dimorphism in *Selaginella* is generally considered to be related to efficient trapping of light in shady habitats with low light intensity. Dengler (1980) noted that certain anatomical features are related to orientation of the shoot to light. Most notably, the abaxial (aligular) epidermis of the dorsal leaf and the adaxial (ligular) epidermis of the ventral leaf consist of nearly isodiametric cells, each containing a single large chloroplast. These surfaces are directed toward light. The shad-